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Warm winters reduce landscape-scale variability in the duration of egg incubation for coho salmon (*Oncorhynchus kisutch*) on the Copper River Delta, Alaska

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Abstract: We quantified the sum of daily mean temperature above 0 °C and modeled incubation duration using water temperature data collected at 12 coho salmon (*Oncorhynchus kisutch*) spawning sites during two incubation periods with cool, snow-dominant conditions and three incubation periods with anomalously warm, rain-transitional conditions, a proxy for a future climate scenario. Warmer water temperatures during warm–rain-transitional winters yielded a 58-day reduction in the median duration of egg incubation; however, the magnitude of change at individual sites varied widely and was controlled by water source. At groundwater-fed sites, temperature variations were strongly attenuated, leading to small interannual differences in incubation duration that were relatively insensitive to short-term changes in air temperature. In contrast, modeled incubation duration was shortened by up to 3 months during warm–rain-transitional winters at precipitation-fed sites. Remarkably, our modeling showed increased uniformity in incubation duration across the landscape during warm–rain-transitional winters. The potential loss of diversity in incubation duration during warmer winters, in isolation, may reduce portfolio effects in this region's coho salmon population by promoting greater synchronization in the time of spawning.

Résumé : Nous avons quantifié la somme des températures moyennes quotidiennes supérieures à 0 °C et modélisé la durée d'incubation en utilisant des données sur la température de l'eau obtenues dans 12 lieux de frai de saumons cohos (*Oncorhynchus kisutch*) durant deux périodes d'incubation caractérisées par des conditions froides dominées par la neige et trois périodes d'incubation caractérisées par des conditions pluvieuses anormalement chaudes de transition, représentant un scénario de climat futur. Les températures de l'eau plus élevées durant les hivers chauds et pluvieux de transition entraînent une baisse de 58 jours de la durée médiane d'incubation des œufs; l'ampleur du changement dans chaque lieu de frai varie toutefois considérablement et est contrôlée par la source d'eau. Aux sites alimentés par de l'eau souterraine, les variations de température sont fortement atténuées, menant à de faibles différences interannuelles de la durée d'incubation relativement insensibles aux changements à court terme de la température de l'air. En revanche, la durée d'incubation modélisée est de jusqu'à 3 mois plus courte durant les hivers chauds et pluvieux de transition dans les sites alimentés en eau par les précipitations. Fait à noter, la modélisation fait ressortir une uniformité accrue de la durée d'incubation à l'échelle du paysage durant les hivers chauds et pluvieux de transition. La baisse potentielle de diversité des durées d'incubation durant les hivers chauds pourrait, en soi, réduire les effets de portefeuille dans la population de saumons cohos de la région en favorisant une plus grande synchronisation du moment du frai. [Traduit par la Rédaction]

Introduction

Climate change is already affecting water temperature in freshwater ecosystems that support Pacific salmon (*Oncorhynchus* spp.) and other cold-water fishes (Schindler et al. 2005; Isaak et al. 2012). Growth and metabolic rates for ectothermic aquatic organisms, including Pacific salmon (Beer and Anderson 2011; Crozier and Hutchings 2014) and their primary prey species (Gerten and Adrian 2000; Durance and Ormerod 2007), are largely controlled by water temperature. Much of the research examining the potential impacts of changing thermal regimes in cold-water ecosystems has focused on summer temperatures, when annual thermal maxima may exceed tolerance thresholds for cold-water fishes. However, quantifying the influence of climate change on water temperature during the autumn, winter, and spring months, the

"cool season" at northern latitudes, may also be important, because physiology and behavior have adapted to the constraints of winter conditions (Shuter et al. 2012).

The embryos of most Pacific salmon incubate throughout the cool season. Incubation temperature influences egg-to-fry survival, incubation duration, and size at emergence (Murray and McPhail 1988). Spawn timing is finely tuned to local environmental conditions, notably water temperatures during the incubation period (Beacham and Murray 1990), to promote juvenile emergence at a favorable time of year for growth and viability (Brannon 1987; Webb and McLay 1996; Brannon et al. 2004). Increases in water temperatures during the incubation period can accelerate development and may trigger cascading effects on growth, viability, and seaward migration timing for juvenile anadromous sal-

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monids (Jonsson et al. 2005; Finstad and Jonsson 2012). Rising water temperatures associated with climate change may accelerate incubation, affecting salmon life-history expression and resilience (Crozier et al. 2008). Understanding the scale and magnitude of potential warming effects on the early life-history stages may be critical for anticipating the overall impacts of climate change on anadromous salmonids.

Quantifying climate change effects on water temperature at incubation sites remains a challenge due to spatial and temporal variability in the climatic (Hilderbrand et al. 2014), physiographic (Mayer 2012; Luce et al. 2014), and geomorphic (Leach and Moore 2011; Kelleher et al. 2012) factors that control water temperature. For example, advection and conduction of heat through the streambed interface as a result of hyporheic exchange (Arrigoni et al. 2008; Hannah et al. 2009; Gariglio et al. 2013), upwelling groundwater (Brown et al. 2005; O'Driscoll and DeWalle 2006), and lateral stormflow (Kobayashi et al. 1999; Leach and Moore 2014) can influence stream temperature, particularly in small streams and during the winter months when net radiative and sensible heat fluxes at the water's surface are strongly negative (Caissie et al. 2014).

Snowmelt and ice melt also exert control over water temperature (Webb and Nobilis 1997; Malard et al. 2001), and the quantity and timing of meltwater inputs are anticipated to change in catchments where the fraction of precipitation that accumulates as snowpack is declining as mean near-surface air temperatures rise (Arismendi et al. 2013; Safeeq et al. 2016). In regions where the mean cool-season air temperature is anticipated to rise above the freezing point, both increasing air temperatures and decreasing snowpack may affect water temperature (Mantua et al. 2010; Null et al. 2013).

One such region is coastal Alaska, habitat for some of the world's most robust Pacific salmon populations, where mean annual air temperature is projected to rise 3–5 °C by 2080, based on midrange emissions scenarios (University of Alaska 2015). Hydrologically important changes in water sources and associated thermal regimes are anticipated, because mean winter air temperature is projected to surpass the freezing point along the coastline, greatly reducing low-elevation snowpack and seasonal ice cover on freshwater bodies (McAfee et al. 2014). Water temperature in rivers in coastal Alaska is generally anticipated to increase in response to the projected increase in air temperature (Kyle and Brabets 2001; Mauger et al. 2017), the reduction in glacier cover (Hood and Berner 2009; Fellman et al. 2014), and the loss of seasonal snowpack (Lisi et al. 2015). However, considerable variability in the magnitude and timing of these effects is likely because of the region's complex geomorphology and physiography, which creates sharp gradients in atmospheric conditions, water sources, and water-residence times. For example, the size, steepness, and elevation of the watershed and the presence of glaciers, lakes, and upwelling groundwater have all been correlated with water temperature in salmon-bearing streams in Alaska (Lisi et al. 2013; Adelfio 2016; Winfree et al. 2018).

In this study, we used surface and shallow streambed water-temperature monitoring data collected at coho salmon (*Oncorhynchus kisutch*) spawning sites on the Copper River Delta (hereinafter CRD) in southcentral Alaska to examine how winter climate conditions affect water temperature. The southern coast of Alaska experienced pervasive and record-setting warm weather from June 2013 to September 2016 (Thoman and Brettschneider 2016; Walsh et al. 2017), providing an opportunity to observe changes in incubation conditions during anomalously warm winters with precipitation dominated by rainfall and transient seasonal snow and ice cover (warm–rain-transitional), conditions that are anticipated to become increasingly common (Littell et al. 2017). We compared how differences in water temperatures during cool–snow-dominant and warm–rain-transitional winters influenced the duration of incubation in streams with different water sources.

Materials and methods

Study area

The CRD (Fig. 1), a low-relief coastal foreland between the Gulf of Alaska and the Chugach Mountains, has complex geomorphology shaped by glacial activity (Barclay et al. 2013), marine and tectonic forces (Reimnitz 1966; Plafker 1990), and high rates of fluvial sedimentation (Jaeger et al. 1998). Deposits of glaciomarine and fluvial sediment are up to 180 m thick (Reimnitz 1966). Layers of outwash deposits, sediment transported by distributaries of nearby glaciers, cover most of the subaerial deltaic surface below glaciated valleys that bisect the Chugach Mountains.

The relatively coarse glacial alluvium provides an appropriate structure for alluvial aquifers, which are recharged by abundant annual precipitation and meltwater from snowpack and glaciers (Dorava and Sokup 1994). The layers of glacial alluvium thin toward their seaward extent, likely driving the groundwater upwelling that feeds small spring creeks and augments baseflow into certain reaches of larger precipitation-fed rivers. Similar hydrologic connectivity has been observed on glacial outwashes around the world (Ward et al. 1999; Robinson et al. 2008; Crossman et al. 2011).

Piedmont areas, where shallow till or peat is underlain by sedimentary or extrusive igneous bedrock, are located between glacial outwashes and adjoin the Chugach Mountains (Wilson et al. 2008). The structure and morphology of the piedmont is not believed to be conducive for storing large quantities of groundwater, and we have not observed upwelling groundwater in these catchments. Despite the range of geomorphic conditions exhibited across the CRD, cold-water fishes, particularly coho salmon, are widely distributed and use streams in both the outwash and piedmont areas for spawning.

The CRD is characterized by a subarctic maritime climate. The 1981–2010 climatic normal was cool (4 °C mean annual air temperature) and wet (235 cm precipitation·year⁻¹), with mean monthly air temperatures below freezing (–0.4 to –3.0 °C) from November through March (National Oceanic and Atmospheric Administration (NOAA), Global Historic Climatology Network, weather station #26410 located within the study area). Winter air temperatures exhibited substantial interannual variability and were strongly influenced by the Pacific Decadal Oscillation (PDO). We calculated the shift from the cool to warm phase of the PDO in 1977 resulted in a 1.6 °C increase in mean winter temperature.

Climate models project an average surface air temperature increase of 5 °C for the CRD by the year 2100 under the Representative Concentration Pathway 6.0 greenhouse gas emissions scenario, with the greatest warming in the winter months (University of Alaska 2015). Mean monthly near-surface air temperatures are anticipated to exceed freezing throughout the entire year by 2050, contributing to a 20%–40% reduction in mean snowpack snow-water equivalent (SWE) below 500 m elevation on the CRD (Littell et al. 2017), a change that is anticipated to reduce the mean ratio of peak (1 April) SWE to cool season (October–March) precipitation from 0.30 to 0.15. At the highest elevations of the study area (500–1500 m), a seasonal reduction in SWE is projected for late autumn (October–November), but annual SWE is anticipated to remain within ±10% of historic condition (Littell et al. 2017), suggesting climate change effects on water sources may vary with catchment hypsometry.

Study catchment characteristics

We collected surface (stream) and shallow streambed (intergravel) water temperature data at 12 coho salmon spawning and rearing sites, each in a unique catchment on the CRD. The study sites were located between 5 and 48 m above sea level. Using

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Fig. 1. Study site and weather station locations on the Copper River Delta, Alaska, USA. Study catchments were interpolated from surficial topography using a 5 m resolution digital elevation model produced and distributed by the US Geological Survey. The hillshade layer was generated from a 20 m resolution digital elevation model produced by SPOT Image Corporation and obtained from the US Forest Service.
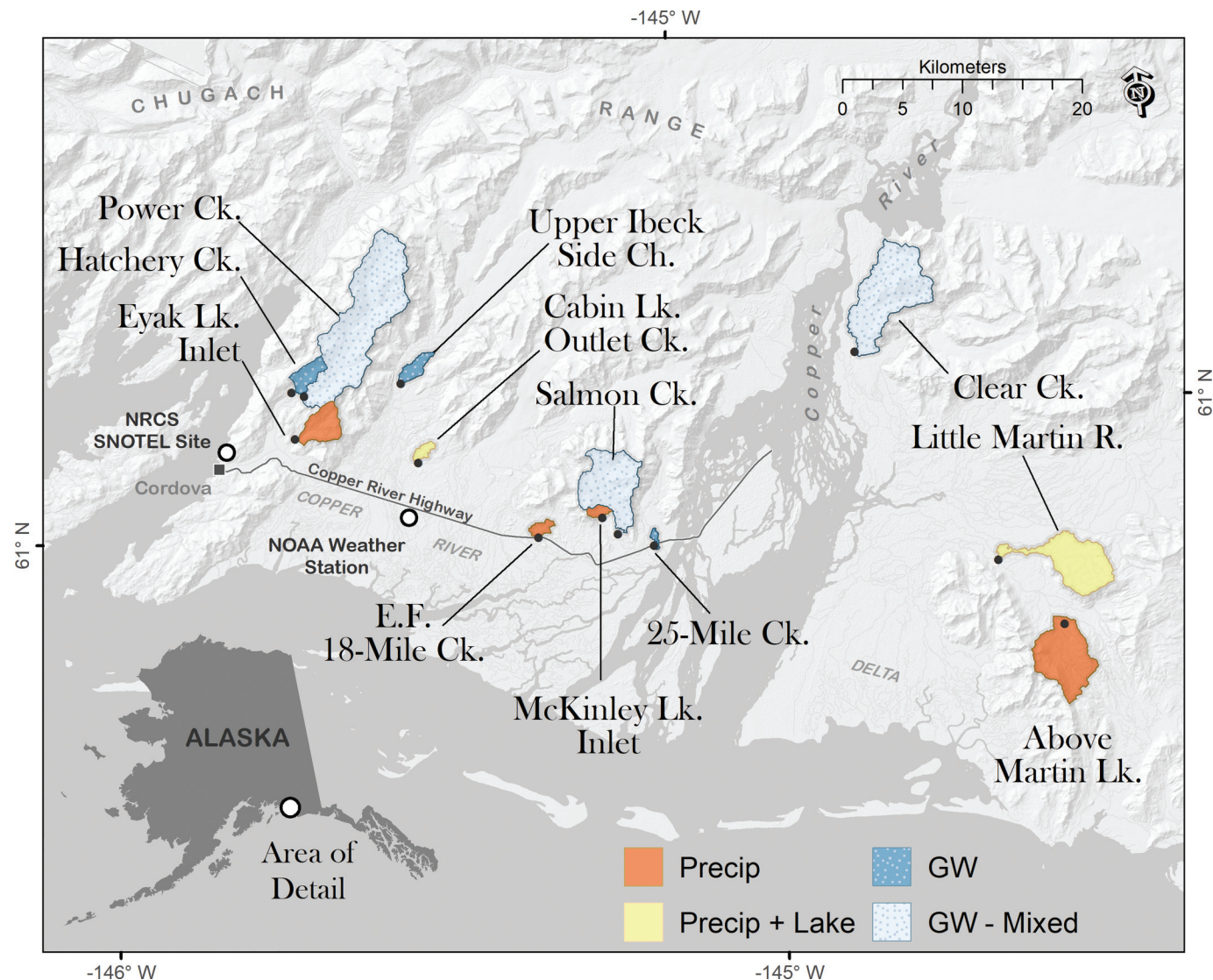
spatial analyst tools in ArcGIS 10.3 (Environmental Systems Research Institute, Redlands, California, USA), we interpolated catchment boundaries based on surficial topography from the US Geological Survey (USGS) interferometric synthetic aperture radar (IFSAR) 5 m digital elevation model. The study catchments varied in total area (61 to 5426 ha), mean elevation (25 to 622 m), and mean slope (3 to 28 degrees). Surficial geology was variable, with glacial outwash deposits present in nine catchments (Wilson et al. 2008).

We calculated lake and ice cover with data from USGS National Hydrography Dataset. Five catchments contained shallow lakes and ponds, but in only two catchments (Little Martin River and Cabin Lake Outlet) did lake area exceed 5% of total area (15.4% and 6.4%, respectively; Table 1). The three highest-elevation catchments (Power Creek, Salmon Creek, and Clear Creek) had perennial ice cover (12.7%, 7.2%, and 1.8% of catchment area, respectively). Two sites (McKinley Lake Inlet and Eyak Lake Inlet) were located at the mouths of inlet streams, within the range of influence of lakes.

Six sites were anticipated to have upwelling groundwater (Table 1) because of unusually cold summertime water temperatures. The groundwater influence was confirmed during piezo-meter installation, when we observed strongly positive vertical head gradients through the streambed. Subsequent water-temperature measurement showed these streams had low diel and annual variance in temperature, supporting evidence of groundwater dominance (Middleton et al. 2016).

Water-source categories

We divided the study sites into four categories that describe the dominant water source: groundwater (GW), groundwater-mixed (GW-Mixed), precipitation (Precip), and precipitation with a lake upstream (Precip+Lake). The GW sites were upwelling spring creeks in small (<454 ha) catchments with a low mean elevation. GW sites had stable hydrographs with relatively small contributions from rain and seasonal snowmelt. The GW-Mixed sites were located in large (2267–5426 ha) "U-shaped" mountain valleys with high mean catchment elevations and perennial ice in the headwaters. Upwelling groundwater contributed to baseflow, particularly in the winter months; however, precipitation and meltwater from glaciers and seasonal snowpack provided most of the annual water flow at GW-Mixed sites. In contrast, sites in the Precip and Precip+Lake categories drained piedmont catchments that lacked

Table 1. Location and description of catchment characteristics for the 12 study sites.

Thermal sensitivity category	Site information				Catchment physiography			
	Site name	Latitude (°N)	Longitude (°W)		Area (ha)	Lake area (%)	Glacier area (%)	Mean elevation (m)
Precip+Lake	Cabin Lk. Outlet Ck.	60.53	145.46		166	6.7	0.0	83
	Little Martin R.	60.40	144.61		2156	15.4	0.0	158
Precip	E. Fk. 18-Mile Ck.	60.46	145.29		188	0.0	0.0	33
	Above Martin Ck.	60.34	144.52		2274	1.3	0.0	271
	McKinley Lk. Inlet	60.47	145.19		155	0.0	0.0	224
	Eyak Lk. Inlet	60.56	145.64		792	0.0	0.0	433
GW-Mixed	Clear Ck.	60.57	144.78		3504	0.3	1.8	337
	Power Ck.	60.59	145.62		5426	0.0	12.7	622
	Salmon Ck.	60.45	145.17		2267	0.1	7.2	388
GW	Hatchery Ck.	60.59	145.64		454	0.0	0.0	308
	Upper Ibeck Side Ch.	60.59	145.47		336	0.0	0.0	74
	25-Mile Ck.	60.44	145.12		61	0.0	0.0	25

perennial ice cover. Rainfall and seasonal snowmelt moved through the catchment quickly, creating a "flashy" hydrograph with low baseflows and high storm peaks. In contrast with the Precip sites, more than 5% of the upstream catchment area at the Precip+Lake sites was occupied by broad, shallow lakes, which have been demonstrated to influence water temperature elsewhere in coastal Alaska (Lisi et al. 2013; Fellman et al. 2014).

Temperature data collection

We monitored surface (stream) and streambed (intergravel) water temperatures hourly from 1 October 2011 (start of water year 2012) through 30 September 2016 (end of water year 2016) using data loggers with ±0.2 °C sensor accuracy (Onset Computer Corporation, Bourne, Massachusetts). We recorded surface-water temperature at each site with 1 HOBO Pro v2 data logger housed in a 15 cm long section of 4.1 cm internal diameter galvanized steel pipe to shade the sensor and protect it from physical damage. Surface-water temperature loggers were placed at the bottom of the water column. Deployment depths were at least 20 cm, typically 50 to 60 cm, at average summer water flows, and the surface water at each study site was assumed to be well mixed by turbulent flow.

We measured streambed water temperature 50 to 70 cm into the streambed, using two interchangeable techniques: (*i*) a Pro v2 data logger installed behind a 10 cm long screen near the bottom of a 101 cm long piezometer with a foam baffle located above the screened section to limit vertical water flow or (*ii*) a TidbiT v2 data logger installed directly into the substrate after boring a hole with a custom-made driver (Zimmerman and Finn 2012). We deployed two streambed loggers at each site using one or both methods.

Burial depth for coho salmon eggs ranges between 8 and 55 cm and is correlated with size of the maternal female (van den Berghe and Gross 1984; DeVries 1997). By measuring water temperature at the stream bottom and 50 to 70 cm into the streambed, we bracketed the potential range of incubation temperature experienced by eggs at each location.

We downloaded data loggers every 6 to 12 months throughout the study period. We removed erroneous values, including unreasonable outliers (which suggest sensor error) and abnormally high hourly variance (>3 °C), suggesting the sensor was exposed to air. Occasional data gaps occurred when streambed data loggers were exposed to surface water, when surface-water loggers were exposed to air, and when data loggers were lost or malfunctioned. We filled gaps in the surface-water time series at four sites by fitting a linear regression between streambed and surface-water temperature and calculating daily average surface-water temperatures from the daily average streambed temperatures. In all cases, adjusted R^2 was 0.7 or greater, and the modeled data composed 12% to 45% of the total time series. Gaps in the streambed

data-logger time series, which were particularly common at Power Creek owing to a channel shift in the study reach, were left unfilled.

Using hourly temperature data, excluding days with fewer than 20 measurements, we calculated daily mean temperature for each data-logger location at each site. We calculated weekly (7-day, "non-rolling") and monthly mean temperatures for surface-water temperatures at each site from the daily mean temperature, excluding weeks with fewer than 7 days of data and months with fewer than 21 days of data.

**Thermal sensitivity analysis**

We regressed weekly mean surface-water temperatures against weekly mean air temperatures, which we calculated from daily temperature averages observed at NOAA GHCN weather station #26410, located near sea level within the study area (Fig. 1). Although localized air temperature departures were likely, previous work has shown that regional temperatures are acceptable for this type of analysis (Mohseni et al. 1998; Caldwell et al. 2015). To assess correlation between water temperature (dependent variable) and air temperature (independent variable) for all weeks with a mean air temperature exceeding 0 °C, we fitted a simple linear regression model with coefficients for intercept and slope.

Linear models have frequently been applied to correlate water and air temperatures (see Benyahya et al. 2007 for a review). The slope has been used as a metric to describe "thermal sensitivity" (Kelleher et al. 2012), the expected change in water temperature per unit change in air temperature, and is useful for making comparisons across catchments and landscapes (Mantua et al. 2010; Mayer 2012; Snyder et al. 2015). Note, however, that thermal sensitivity does not imply that the change in air temperature is causing the change in water temperature (see Caissie 2006 for a review).

Winter types

We divided the 5 study years into two winter types, "cool–snow-dominant" and "warm–rain-transitional", based on October through May surface air temperature at the NOAA weather station near sea level, April mean snowpack SWE depth at Mt. Eyak Snow Telemetry (SNOTEL) site #1073 (USDA National Resources Conservation Service) located at 425 m elevation in the study area, and the fraction of total October to March precipitation contained in snowpack as SWE on 1 April at the Mt. Eyak SNOTEL site. Water years 2012 (WY2012) and WY2013 were anomalously cool from October through May (Fig. 2a) and accumulated above average SWE relative to the 2006–2016 period of record (Fig. 2b). These two winters were classified as cool–snow-dominant and the October to April SWE-to-precipitation ratio exceeded 60% at the Mt. Eyak SNOTEL site (Fig. 2c). Further, sea-level snowpack and persistent

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Fig. 2. (*a*) Anomalies (°C) from the 1981–2010 mean temperature between 1 October and 31 May for the 72-year period of continuous record at an NOAA weather station located at 13 m elevation within the study area; (*b*) mean April snow water equivalent (SWE); and (*c*) ratio of snow water equivalent on 1 April to total precipitation between 1 October and 31 May for the 11-year period of record at an NRCS SNOTEL station located at 425 m elevation within the study area.
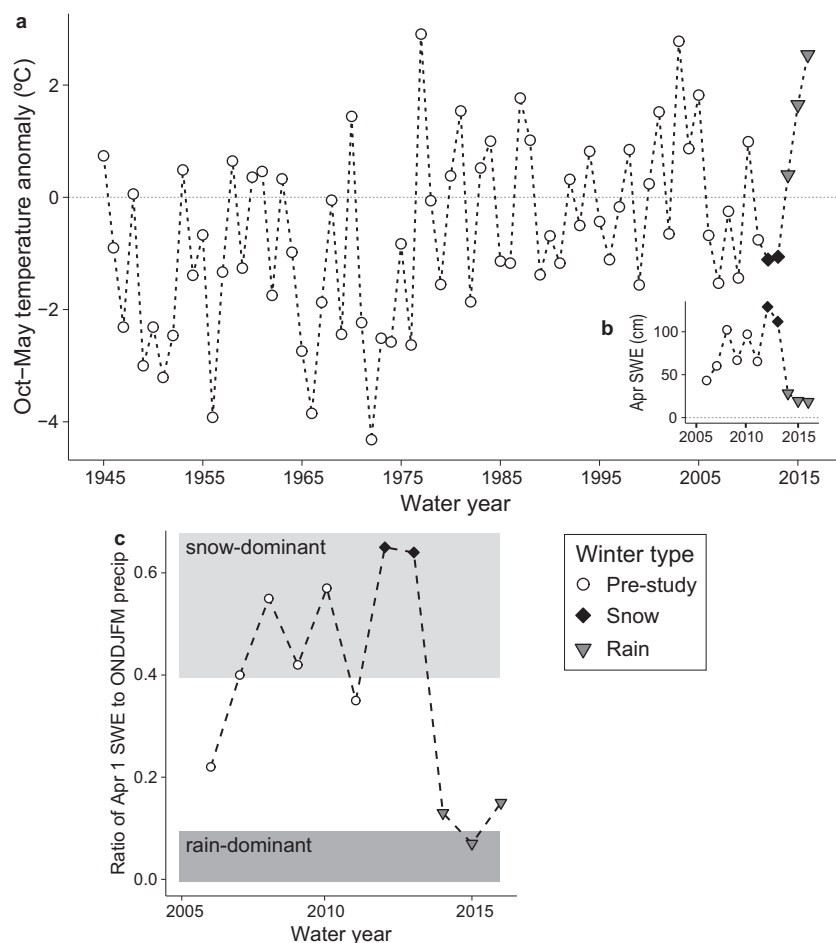
waterbody ice were also observed in the study catchments. During the preceding cool-phase PDO (1947–1976), October through May air temperatures on the CRD measured 1.5 °C cooler than they did during the climatic "normal" period of 1981–2010, and very cold winters were common. The conditions occurring during the two snow-dominated winters in this study (WY2012 and WY2013) would have been slightly warmer than the average conditions for 1947–1976.

Conditions were noticeably mild during the three warm–rain-transitional winters (WY2014 through WY2016). Sea-level snow cover was nearly absent, and April snowpack SWE at 425 m was as much as 70 cm less than the period-of-record average. Air temperatures were anomalously warm, particularly during WY2015 and WY2016, when October through May mean air temperatures were the second and sixth warmest observed in the 71-year record. Less than 20% of the October to April precipitation accumulated as snowpack at the Mt. Eyak SNOTEL site. The warm–rain-transitional winters examined here, especially WY2015 and WY2016, were warmer than any single winter season during the previous cool phase of the PDO; however, the conditions resulting in warm–rain-transitional winters occurred more frequently during the most recent warm phase of the PDO (1977–1998).

Accumulated thermal units (ATU) analysis

ATU were calculated from the cumulative sum of the daily mean temperature (°C) during the assumed coho salmon incubation period, which we defined as the 243 days between 1 October

and 31 May (29 February was excluded), based on presumed mean spawning and emergence dates. We recognize that actual spawning and emergence dates were likely to vary at each site as well as interannually. Our intent here was not to examine the actual incubation period in each stream in each year, but rather to use a standardized time period to examine relative differences in the effects of interannual climatic variability on incubation conditions across sites with different water sources.

For each site, we calculated cumulative ATU for each of the three data-logger locations (one surface and two streambed loggers) when more than 240 days of data were available. We calculated mean total ATU for each 243-day incubation period at each site by averaging the surface-water ATU with the mean of the two streambed ATU measurements. We applied two-factor analysis of variance (ANOVA) using sequential sum of squares (a "type I" analysis) to test for significant differences in mean total ATU. We used Tukey's honest significant differences test to assess the significance of pairwise comparisons across winter types and water-source categories.

To assess landscape-scale variability in total ATU, we calculated the coefficient of variation (CV) among sites. A Welch two-sample *t* test was applied to test the hypothesis that CV was equal during the cool–snow-dominant and warm–rain-transitional winters.

Incubation duration analysis

We calculated incubation duration by applying an empirically derived Bělehrádek model (Alderdice and Velsen 1978) that was

Fig. 3. (*a*) Daily mean water temperature recorded in the surface (orange line) and streambed (blue lines) water and (*b*) monthly mean water temperature recorded in the surface water at 12 study sites during the 5-year study period.
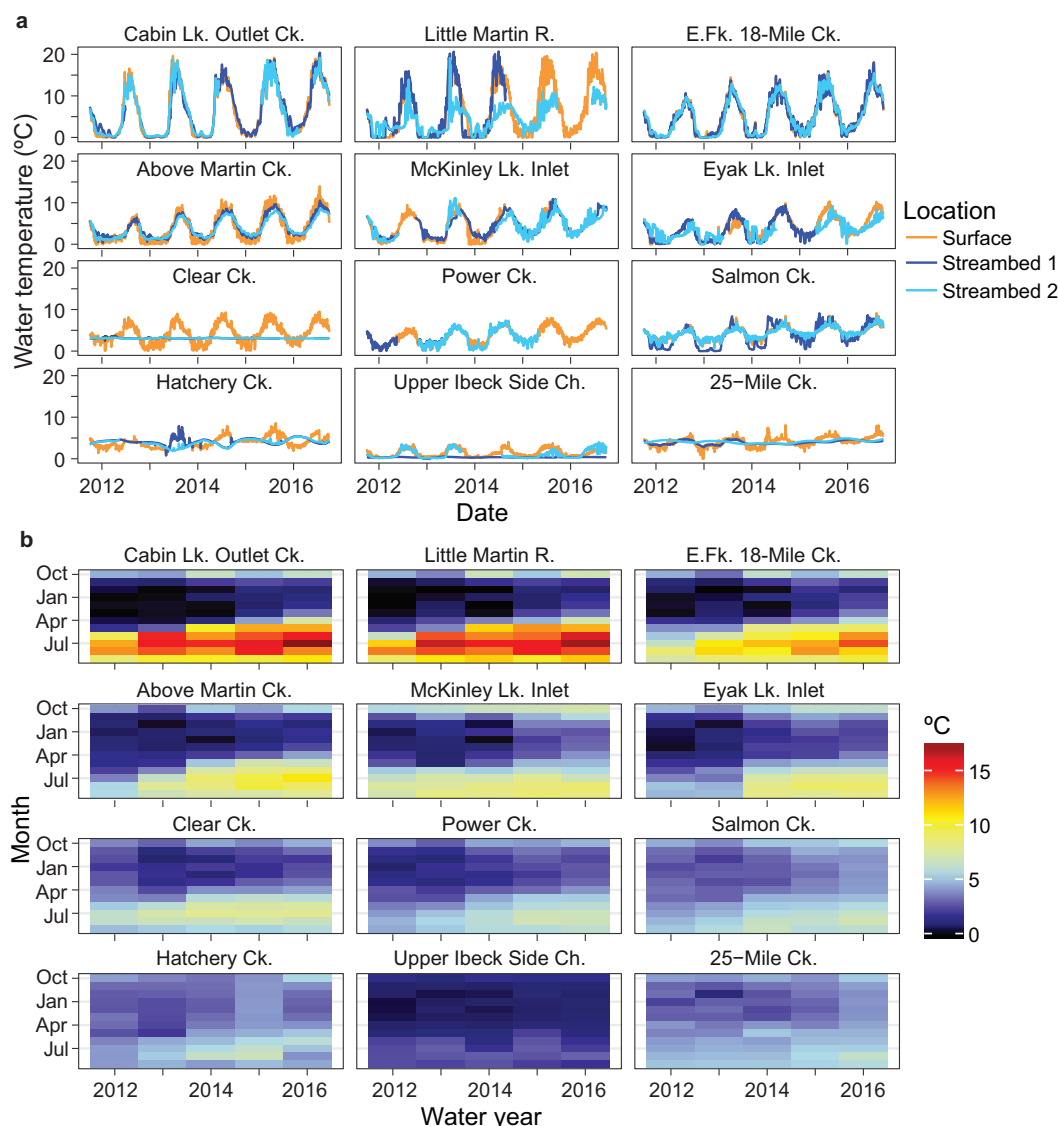
developed by Beacham and Murray (1990) and modified by Sparks et al. (2019). Beacham and Murray fitted 10 models to development data collected for coho salmon embryos and determined the log-inverse Bělehrádek model was among the best-fitting models (r^2 = 0.98) across a range of incubation temperatures (1.5 to 12 °C) and, importantly for our study, performed particularly well at low (1.5 to 3 °C) water temperatures. Sparks et al. modified the Beacham and Murray approach by solving for the inverse of the original function, which they described as the daily "effective value." The effective value model equation is

$$(1) \qquad E_i = \frac{1}{\exp[7.018 - 1.069 \times \log_e(T_i + 2.062)]}$$

where E_i is the relative daily effective value, which has a range of 0–1, and T_i is the daily mean water temperature (°C), which we calculated by averaging the daily mean surface-water temperature with the daily mean streambed water temperature. We calculated the duration of incubation from 1 October, the assumed average spawning date, until the date fry emerge from the gravel (when E = 1), as predicted by the effective value model. A Welch

two-sample t test was applied to test the hypothesis that the duration of incubation was equal during the cool–snow-dominant and warm–rain-transitional winters.

Results

Spatial and temporal water-temperature heterogeneity

Surface and streambed water temperatures exhibited spatial and temporal heterogeneity on daily and monthly time scales (Figs. 3*a*, 3*b*). Linear regression demonstrated that weekly surface-water temperature was strongly correlated with air temperature (Fig. 4*a*; Table 2) at all study sites. The regression slope ranged from 0.16 to 1.29, indicating that the most thermally sensitive site was eight times more sensitive than the least sensitive site.

Geomorphic differences between the sites, captured by the water-source categories, correlated with these differences in thermal sensitivity across the landscape (Fig. 4*b*), suggesting that differences in water sources and geomorphology are responsible for the observed landscape-scale temperature heterogeneity. Sites with shallow lakes upstream (Precip+Lake) were most sensitive to air temperature, whereas sites in small, low-elevation catchments with upwelling groundwater (GW) were the least sensitive. Sites

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Fig. 4. (*a*) Linear regressions (black lines) relating observations of weekly average air temperature to weekly average surface-water temperature (gray points) and (*b*) thermal sensitivity related to dominant water source for all 12 study sites.
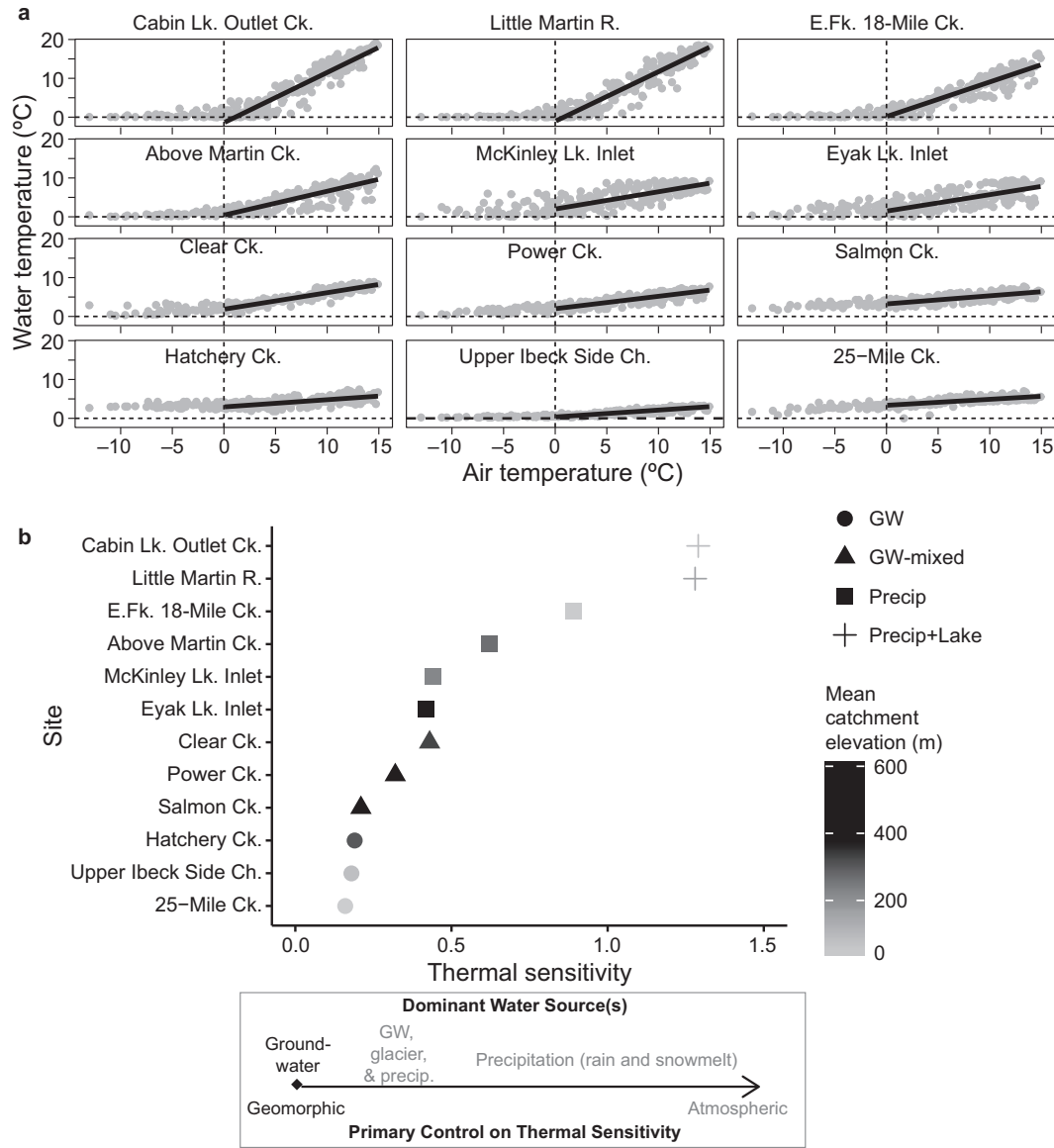

Table 2. Coefficients and fit, as indicated by adjusted r^2 and root mean square error (RMSE), for linear regressions correlating weekly mean air and surface-water temperature at the study sites.

Thermal sensitivity category	Site name	Linear regression fit			
		Slope	y intercept	Adjusted r^2	RMSE
Precip+Lake	Cabin Lk. Outlet Ck.	1.29	−1.43	0.90	1.89
	Little Martin R.	1.28	−1.06	0.89	1.93
Precip	E. Fk. 18-Mile Ck.	0.89	0.14	0.86	1.53
	Above Martin Ck.	0.62	0.43	0.73	1.60
	McKinley Lk. Inlet	0.44	2.00	0.56	1.70
	Eyak Lk. Inlet	0.42	1.46	0.52	1.77
GW-Mixed	Clear Ck.	0.42	1.85	0.86	0.72
	Power Ck.	0.32	1.98	0.75	0.80
	Salmon Ck.	0.21	3.22	0.56	0.79
GW	Hatchery Ck.	0.19	2.94	0.45	0.88
	Upper Ibeck Side Ch.	0.18	0.35	0.77	0.42
	25-Mile Ck.	0.16	3.35	0.52	0.64

Fig. 5. (*a*) Accumulated thermal units (ATU) between 1 October and 31 May; (*b*) total (October through May) ATU recorded at each of 12 study sites in each incubation period over 5 years; and (*c*) coefficient of variation for total ATU for all sites by winter type.
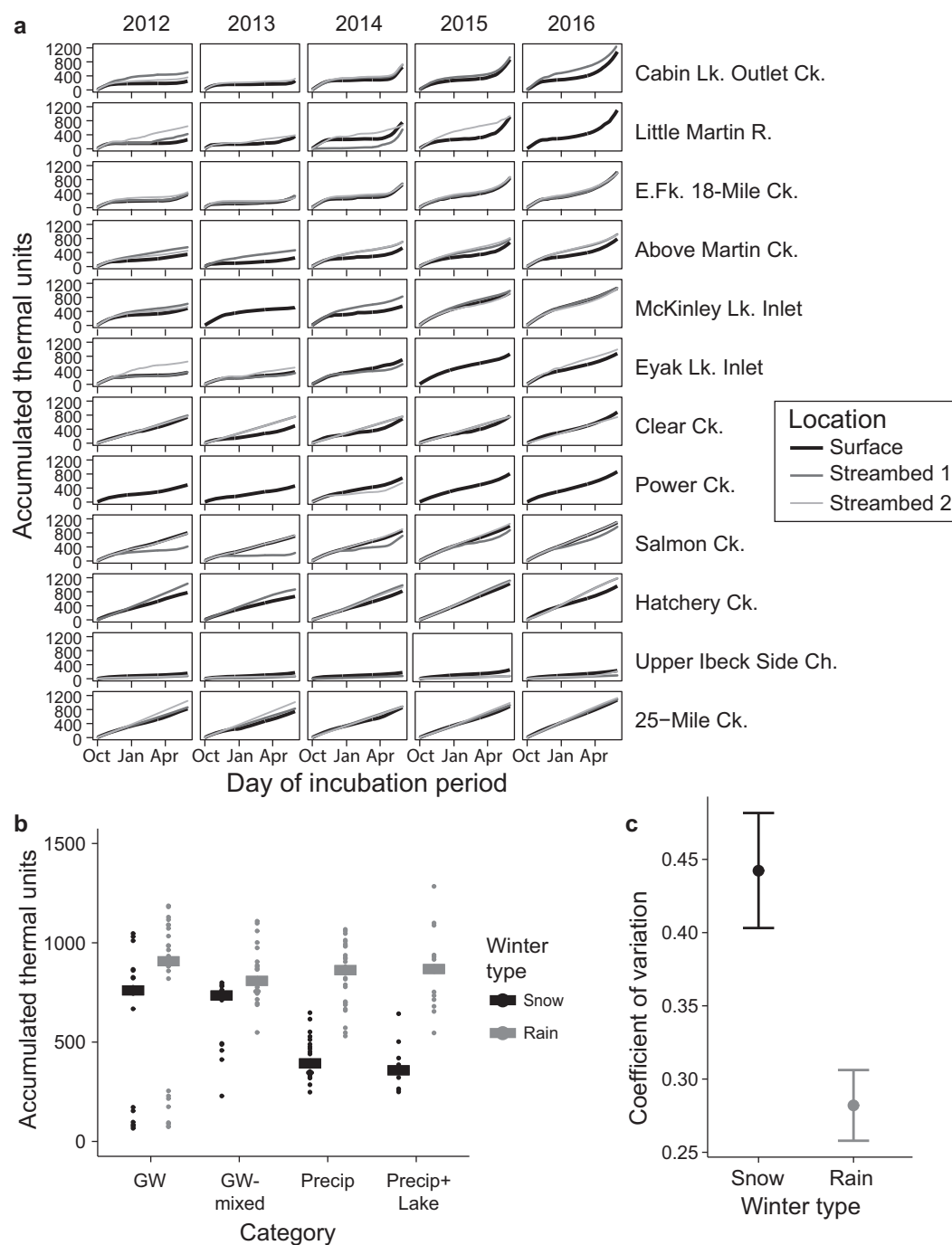
with mixed groundwater, glacial, and precipitation water sources (GW-Mixed) were less sensitive than sites with precipitation water sources (Precip).

Accumulated thermal units

The rate and the magnitude of October–May thermal unit accumulation exhibited spatial and temporal heterogeneity (Fig. 5*a*). Significantly more ATU were acquired during warm–rain-transitional winters, when snowpack was greatly reduced ($p < 0.0001$); however, the magnitude of the changes varied by water source (Fig. 5*b*). The sites with the highest thermal sensitivity had the lowest ATU during the cool–snow-dominant winters, but these

sites also warmed the most during the warm–rain-transitional winters.

The greatest differences occurred at the Precip and Precip+Lake sites, where mean ATU was significantly increased ($p < 0.01$) by 98% and 161%, respectively, during warm–rain-transitional winters as compared with cool–snow-dominant winters. In contrast, at GW and GW-Mixed sites, we observed more modest increases in mean ATU (17% and 38%) during the warm–rain transitional winters, and these increases were not statistically significant ($p > 0.59$). As a consequence of these differences, the among-site CV in ATU was significantly higher ($t = 25.04$, df = 2.87, $p < 0.0002$) during the

Fig. 6. Incubation duration in days calculated with the effective value model during two snow-dominant winters (dark squares) and three rain-transitional winters (light circles) (*a*) superimposed on the Beacham and Murray log-inverse model, with a vertical short-dashed line indicating the 1 °C threshold for coho salmon development and long-dashed lines indicating the location of the median for each winter type calculated using all study sites; (*b*) boxplots showing 25% and 75% quantiles, medians (horizontal bars), and range (vertical bars) excluding data from the Upper Ibeck Side Channel; and (*c*) the departure from the 5-year mean duration of incubation in days calculated for each year and site combination, grouped by water-source category.
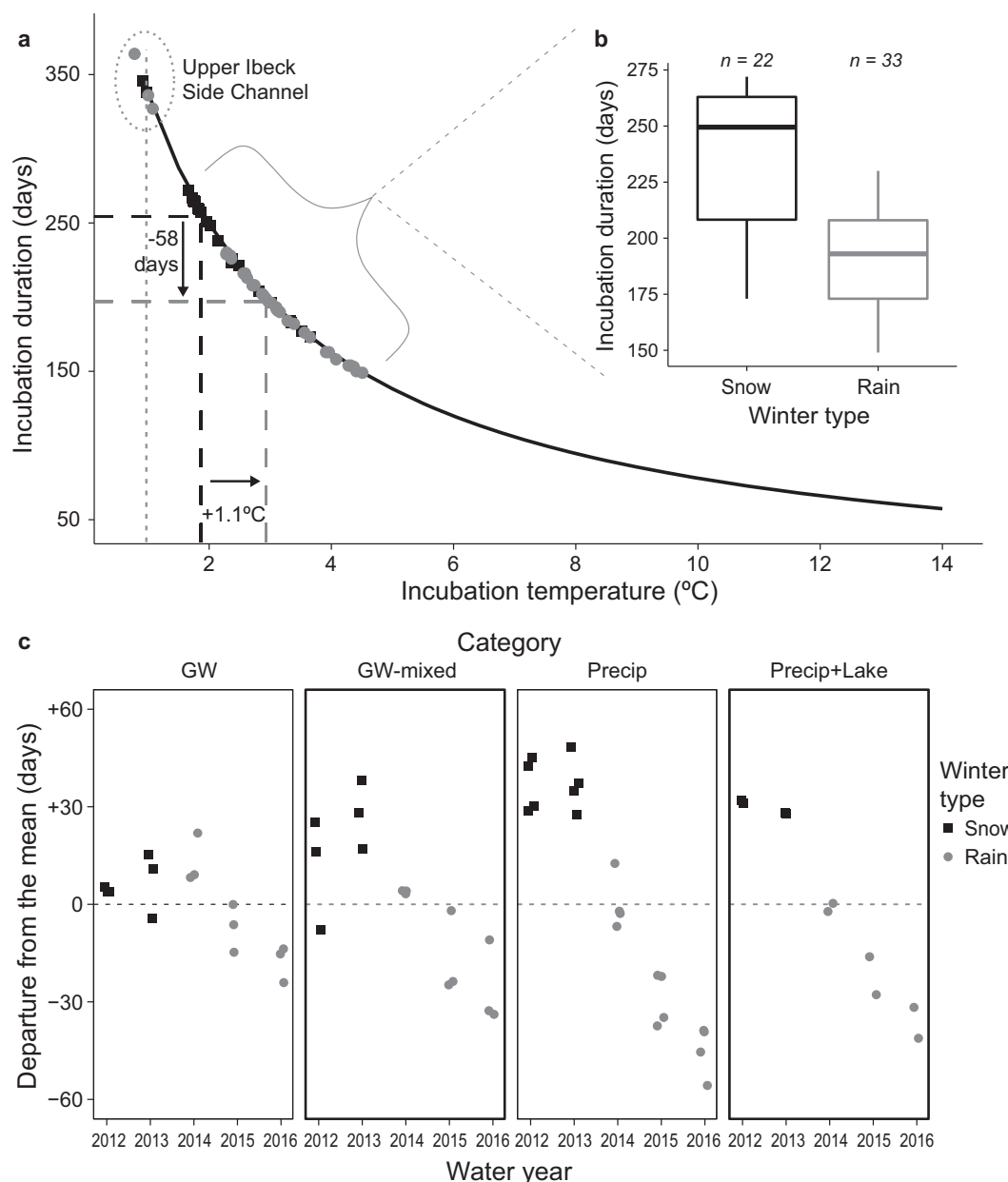
cool–snow-dominant winters, evidence that landscape-scale variability in mean October through May water temperatures was reduced during warm–rain-transitional winters (Fig. 5*c*). Although we performed significance testing and reported *p* values, we also recognize that this study was observational in nature and there were no experimental manipulations. We presented all of our data in Figs. 5*a* and 5*b*, so readers can assess the magnitude of the variability we observed without depending solely on *p* values (Nuzzo 2014).

Incubation duration modeling

The relationship between water temperature and incubation duration is nonlinear, so fewer ATU are required for coho salmon to reach emergence at cooler water temperatures, especially be-

low 5 °C. Owing to this nonlinear relationship and the variability in water temperature across the study area, we observed a 215-day range in the duration of incubation, demonstrating considerable spatial and temporal variability in the incubation environment used by coho salmon (Fig. 6*a*). The duration of incubation was significantly reduced ($t = 3.29$, df = 52.72, $p = 0.002$) during warm–rain-transitional winters, when we observed a 1.1 °C increase in median water temperature that shortened the median duration of incubation by 58 days as compared with the cool–snow-dominant winters.

The coldest site, regardless of winter type, was Upper Ibeck Side Channel, where the mean temperature during incubation was less than 1 °C and incubation was predicted to take up to 1 year,

likely exceeding the lower lethal threshold for coho salmon embryo viability (Dong 1981; Beacham and Murray 1990). Upper Ibeck Side Channel was an outlier, and the duration of incubation was predicted to be 3–7 months shorter at the other 11 sites. The range in the duration of incubation across these 11 sites decreased by 18 days during warm–rain-transitional winters, showing less variability across the landscape as compared with cool–snow-dominant winters (Fig. 6*b*).

The mean duration of incubation was shorter for all water-source categories during warm–rain-transitional winters as compared with cool–snow-dominant winters, but the magnitude of the reduction varied by year and by site (Fig. 6*c*). The smallest differences were observed at the GW sites, where water temperature appeared to lag air temperature by 1–2 years and the mean duration of incubation was only 10 days shorter during the warm–rain transitional winters. In contrast, the greatest differences were observed at the Precip sites, where the mean duration of incubation was 61 days shorter during the warm–rain-transitional winters. Intermediate reductions in mean duration of incubation were predicted for the GW-Mixed (32 days) and, interestingly, the Precip+Lake sites (50 days), which had the greatest increases in October through May ATU.

Discussion

Our results show that geomorphology and water-source types mediated interannual water-temperature variability between winters having cool–snow-dominant conditions in WY2012 and WY2013 and warm–rain-transitional winter conditions in WY2014–WY2016. The sensitivity of water temperature to near-surface atmospheric conditions varied by eightfold among our study sites and was correlated with water sources and catchment geomorphology, as captured by four categories: GW, GW-Mixed, Precip, and Precip+Lake. Sites located in small spring creeks, where groundwater contributed most of the streamflow (GW), and sites with precipitation water sources and broad, shallow lakes upstream (Precip+Lake) were at opposite ends of the water-temperature sensitivity spectrum. At GW sites, groundwater not only reduced summer maximum temperatures, but also provided a thermally stable incubation environment that did not freeze. In contrast, thermal sensitivity and interannual variability in ATU over the incubation period were highest at our two Precip+Lake sites.

We observed an 8 °C difference in mean May water temperature at Precip+Lake sites between cool–snow-dominant and warm–rain-transitional winters, coinciding with a 3 °C difference in mean May air temperature and a 2.6 °C difference in mean October through May air temperature. We hypothesize that broad, shallow lakes amplify water-temperature responses to changing weather and snow and ice cover, particularly during the spring (March to May). At these sites, waterbody ice cover at the end of cool–snow-dominant winters substantially reduced solar heating in spring, and springtime snowmelt and ice melt provided a cold input, maintaining low late-spring and early-summer water temperature at our measurement sites that were downstream from lakes. In contrast, meteorological conditions during warm–rain-transitional winters limited the accumulation of snow and prevent ice formation on the CRD, reducing or eliminating springtime meltwater input and exposing the shallow lakes to short-wave radiation with the onset of long, subarctic spring days. The net effect of the observed springtime warming after warm–rain-transitional winters at Precip+Lake sites was captured by the two- to threefold increases in October through May ATU. However, because most of this warming occurred toward the end of the incubation period, the effects on the duration of incubation were not as pronounced, and Precip+Lake sites had smaller reductions in incubation duration than the Precip sites, despite greater thermal sensitivity.

Our observations align with the findings of other studies that have correlated thermal sensitivity with the same catchment characteristics we used to define our water-source categories, notably, area (Hrachowitz et al. 2010), mean elevation (Lisi et al. 2015), groundwater upwelling (Kelleher et al. 2012; Johnson et al. 2014), upstream lake area (Lisi et al. 2013), and perennial ice cover (Fellman et al. 2014). Heterogeneity in thermal sensitivity is important because it suggests that climate change effects on water temperature in cold-water fish habitats will be spatially variable (Lisi et al. 2015), particularly across landscapes with complex geomorphology.

We found that heterogeneity in thermal sensitivity extended into the incubation environment of a fall-spawning cold-water fish. Here, we discuss three of our observations that have important implications for anticipating effects of climate change on Pacific salmon: (*i*) Upwelling groundwater attenuated changes in water temperature during the coldest months of the year. (*ii*) Model-predicted incubation duration varied with the intensity of winter conditions, but the magnitude of variability was controlled by water sources and catchment geomorphology. (*iii*) Landscape-scale variability in the accumulation of thermal units and the duration of incubation were greater during cool–snow-dominant winters than during warm–rain-transitional winters at our CRD study sites.

Upwelling groundwater

At GW sites, upwelling groundwater attenuated thermal sensitivity and variability in ATU during the cool season (October through May), when salmon eggs were incubating. In addition to reducing summer maximum water temperatures, upwelling groundwater provided a thermally stable incubation environment that remained above freezing, even during prolonged cold spells. Further, cool-season water temperature at GW sites did not vary between cool–snow-dominant and warm–rain-transitional winters, suggesting that incubation conditions may remain relatively consistent despite climate variability. Fall-spawning Pacific salmon have been found to concentrate reproductive efforts at upwelling groundwater sites (Lorenz and Filer 1989; Curran et al. 2011), perhaps, in part, because of this cool-season thermal stability.

The effect of upwelling groundwater on stream temperature is influenced by residence time within the ground (Tague et al. 2008), the magnitude of groundwater flux (Middleton et al. 2016), and distance downstream from the zone of upwelling groundwater (Nichols et al. 2014). For example, we observed significantly different incubation-period water temperatures during cool–snow-dominant and warm–rain-transitional winters at GW-Mixed sites, glacially influenced streams in which groundwater augments baseflow. This observation suggests that either changes in the relative amount of water from each source or changes in the temperature of the non-GW source may influence the thermal environment in these streams. We also observed that GW-Mixed sites had the greatest reach-scale spatial variability in water temperature within the shallow streambed, because thermally heterogeneous upwelling groundwater, downwelling surface water, and lateral subsurface stormflows can all influence water temperature patterns in the incubation zone.

The temperature and the volume of groundwater discharge may be influenced by climate change. Persistent surface warming can increase groundwater temperature in small and shallow unconfined aquifers (Kurylyk et al. 2014, 2015). We have not examined groundwater ages at our study sites, but the aquifers that discharge into our study reaches are shallow and unconfined, and we anticipate that groundwater temperatures, which hovered near the mean annual air temperature at most GW and GW-Mixed sites, will rise as the climate warms.

Glacier melt can be disproportionately important for groundwater recharge (Liljedahl et al. 2017). Our Upper Ibeck Side Channel site, located 3 km from the present-day terminus of Scott

Glacier, was situated in a complex braided stream with precipitation, meltwater, and groundwater sources. However, the hourly shallow streambed water temperature was nearly constant at 0.5 °C throughout the duration of our 5-year study, evidence of a strong glacier melt signature in the upwelling groundwater.

The extremely low year-round water temperatures at the Upper Ibeck Side Channel were likely below the threshold for embryo viability of coho salmon (Dong 1981; Beacham and Murray 1990); nevertheless, adults continued to return to this site to spawn. One possible explanation is that coho salmon had a local adaptation that enabled incubation in extremely cold water. Another plausible explanation is that survival of the embryos near our temperature loggers was low, but spawning adults continued to return to the site because incubation was more successful in the adjacent channels, where subsurface-water temperatures were likely warmer than our monitoring site, allowing for successful incubation.

The high proportion of meltwater recharge suggests this site may be particularly vulnerable to changes associated with a warming climate. If glacial extent is reduced in the future, we anticipate that water temperatures may increase, improving conditions for salmon embryos at this site. However, glacier retreat associated with climate change may also reduce water-table elevation and the spatial extent of groundwater-fed channels on glacial outwashes, as has been observed in Iceland (Levy et al. 2015). If the water table falls at Upper Ibeck Side Channel, the loss of spawning habitat or the loss of eggs to desiccation or freezing may offset any gains in productivity associated with warmer water temperatures.

Incubation duration

Our models showed significant reductions in the duration of incubation at GW-Mixed, Precip, and Precip+Lake sites during warm–rain-transitional winters, predicting that juvenile emergence may have occurred up to 3 months earlier following warm–rain-dominant as compared with cool–snow-dominant winters. In a concurrent study, Campbell et al. (2019) examined timing of hatch and emergence of coho salmon on the CRD, contrasting GW and GW-Mixed streams with Precip streams during 2013, a cool–snow-dominant winter. Their results suggested that spawn timing was locally adapted to water source. Peak coho salmon spawning occurred earlier in Precip streams (~September and October) than in GW-Mixed and GW streams (~November and December). The differences in incubation-period water temperature among these streams during a cool–snow-dominant winter resulted in nearly synchronous peak juvenile emergence across all sites in the summer, which coincided with the greatest abundance of prey species.

Our results suggest that changes in the duration of incubation during warm–rain-transitional winters, which are anticipated to increase in frequency and intensity as the climate warms, may desynchronize juvenile emergence timing if there is not a compensating shift in spawn timing. Thus, rising water temperatures correlated with warming winter climate conditions may have biologically significant impacts on Pacific salmon, even during the coldest months of the year and even when maximum water temperatures remain well below critical thresholds recognized by regulatory agencies (McCullough 1999).

Our confidence in the magnitude of modeled reductions in incubation duration was limited by constraints inherent in our modeling approach. Although spawning almost certainly occurred over several weeks at each site, and the timing of peak spawning is known to vary across the study area, we used the date of 1 October as a standardized spawning date for all sites, enabling a direct comparison of relative changes across water-source categories. Further, the coefficients for our model eq. 1 were fitted for populations of coho salmon outside the study area. Regional variation in the relationship between temperature and the rate of embryo development has been observed in sockeye salmon

(*Oncorhynchus nerka*) (Sparks et al. 2017). Our model also did not incorporate family lineage and egg characteristics (Beer and Steel 2018; Fuhrman et al. 2018) or diel variability in water temperature (Steel et al. 2012), variables that can affect the duration of incubation, adding additional uncertainty to our estimates. We suspect this uncertainty was greatest at Precip and Precip+Lake sites, owing to relatively high intra- and interannual thermal variability. Despite these shortcomings, our approach allowed us to assess the relative importance of water source and winter type on the incubation environment.

Integrated hydrologic models (Leppi et al. 2014; Wobus et al. 2015) predicted that the incubation conditions we observed during warm–rain-transitional winters are likely to become more prevalent in coastal Alaska watersheds by 2100. Leppi et al. (2014) used a suite of future climate scenarios to project 1 to 5 °C increases in mean water temperature during the incubation period of coho salmon. Wobus et al. (2015) projected similar increases in mean water temperature at sockeye salmon (*O. nerka*) spawning streams in a Bristol Bay watershed and modeled substantial reductions in the duration of incubation under anticipated future climate scenarios, even despite some groundwater influence at the study sites.

We anticipate that as climate conditions warm, juveniles will either emerge earlier or adults will spawn later in reaches that lack a strong groundwater signature. The net effect of earlier emergence on juvenile viability has been found to depend largely on the condition of the rearing environment. Earlier emergence is generally anticipated to increase the length of the first growing season and overall juvenile growth in streams fed by snowmelt and ice melt (Beer and Anderson 2011; Leppi et al. 2014). Individuals that emerged earlier in the season were more capable of assimilating seasonally abundant large prey items in late summer, increasing growth rates in snowmelt-fed streams in western Alaska (Armstrong et al. 2010). At Carnation Creek, British Columbia, a 6-week reduction in coho salmon incubation duration significantly increased juvenile growth rates (Scrivener and Andersen 1984) and contributed to earlier seaward migration timing; however, earlier outmigration was suspected to decrease overall survival rates for smolts (Holtby 1988).

When life-history traits, such as earlier emergence, are poorly suited for the local environment and viability is reduced, phenotypic responses, such as alteration of spawn timing to ensure a more favorable emergence timing, have been found to occur more rapidly than genetic adaptations that alter embryo development rates (Kinnison et al. 1998). Thus, if earlier emergence reduces viability for coho salmon in streams on the CRD, we anticipate peak spawning may occur later in the year as a short-term response. A longer-term response could involve changes to egg properties such as size and the composition of the yolk (Crozier et al. 2008).

Landscape-scale variability

We observed reduced variability of ATU across our 12 study sites during warm–rain-transitional winters, and as a consequence, our models predicted that the duration of incubation would be more uniform across the landscape. Even after excluding the Upper Ibeck Side Channel site, a cold outlier, the predicted duration of incubation varied by 99 days across the study sites during cool–snow-dominant winters because mean water temperatures during incubation at Precip and Precip+Lake sites were low (1.8 ± 0.2 °C) compared with GW and GW-Mixed sites (2.8 ± 0.6 °C). The Precip and Precip+Lake sites that were the coldest during the cool–snow-dominant winters also warmed the most. In effect, mean water temperature at sites with precipitation water sources "caught up" and, in some cases, surpassed, mean water temperature at the groundwater upwelling sites where temperatures remained relatively stable.

Interestingly, the nonlinear relationship between water temperature and incubation duration (see Fig. 6a) contributed to reduced variability in the duration of incubation observed during warm–rain-transitional winters. Owing to this nonlinearity, we anticipate that variability in incubation duration will continue to decline as water temperatures continue to rise under projected future climate scenarios, particularly if GW sites respond to long-term temperature trends with gradual warming. As water temperatures rise, Upper Ibeck Side Channel and similar reaches with historically cooler than optimal temperatures for salmon production may become increasingly important, as these sites will contribute to landscape-scale variability in the duration of incubation.

The loss of variability in the duration of incubation is potentially concerning because thermal heterogeneity in freshwater habitat has been linked to increased life-history diversity (Holtby et al. 1989; Armstrong et al. 2010) and abundance for Pacific salmon (Ebersole et al. 2003), thereby increasing the availability of salmon to predators (Lisi et al. 2013) as well as contributing to population stability (Schindler et al. 2010). Asynchrony in spawn timing is particularly important for terrestrial and avian consumers (Schindler et al. 2013), and based on our observations, we anticipate spawn timing may become more homogeneous within the study area in response to a warming winter climate.

We caution that assessing the potential implications of rising water temperatures during incubation for salmon life-history diversity will be complex (Angilletta et al. 2008; Crozier et al. 2008). Temperature during incubation cannot be considered independently from other factors. In the freshwater environment, temperature changes are inextricable from other important physical habitat alterations related to climate, including changes to streamflow (Shanley and Albert 2014), streambed scour (Goode et al. 2013; Sloat et al. 2017), and dissolved oxygen concentrations (Fellman et al. 2015; Sergeant et al. 2017). Further, climate warming may induce or exacerbate conflicting selective pressures on different life stages (Crozier et al. 2008). For example, pink salmon (Oncorhynchus gorbuscha) fry emigration (Taylor 2008) and adult escapement (Kovach et al. 2012, 2013) occurred earlier in response to a warming climate and increasing water temperatures at Auke Creek, southeastern Alaska. Early ocean entry may reduce viability, and early migration may increase prespawn mortality owing to warm water temperatures, suggesting these responses may be maladaptive (Crozier and Hutchings 2014).

Changes in the marine environment may mask or amplify changes in freshwater habitat (Schindler et al. 2008). Climate warming will be superimposed over existing patterns of climate variability, notably the PDO in the native range of Pacific salmon (Mantua et al. 1997). The PDO has been strongly correlated with both marine survival of salmon and winter climate in the study area, including near-surface air temperature and quantity of precipitation, two controls on the snowpack-to-precipitation ratio. Understanding how interactions between large-scale climate oscillations and winter temperature and precipitation have affected Pacific salmon life-history expression in the past, as well as how climate variability may influence long-term trends in climate change in the future, will be important. These patterns are unlikely to be simple. In the freshwater environment, they are modulated by water source and catchment geomorphology. For example, we anticipate Precip+Lake and Precip sites will be highly responsive to changes in the prevailing weather, responding to interannual fluctuations, climate oscillations such as the PDO, and trends driven by anthropogenic climate warming. "Thermal complexity" (Steel et al. 2017) in freshwater habitat likely increases Pacific salmon resilience to perturbations in climate and other disturbances. Our findings suggest that managing landscapes to protect and restore thermal heterogeneity in incubation habitats may enhance Pacific salmon resilience to climate warming in regions where the proportion of winter precipitation that accumulates as snowpack is projected to substantially decline as a result of rising near-surface air temperatures.

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